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THE BREEDING BIOLOGY OF BROAD-WINGED AND RED-SHOULDERED HAWKS IN WESTERN NEW YORK

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ABSTRACT.—Nesting Red-shouldered (*Buteo lineatus*; RSH) and Broad-winged Hawks (*Buteo platypterus*; BWH) were studied in 1978–1980 in Chautauqua County, New York. Both species nested predominantly in upland maple-beech-hemlock associations. Six of 18 BWH nests were in larch (*Larix decidua*); 7 of 18 RSH nests were in American beech (*Fagus grandifolia*). BWH nested closer to woodland openings and lower in a tree than RSH although neither difference was statistically significant. RSH began nesting about a month before BWH. In general, BWH produced more young and were more successful than RSH. Both species suffered similar types of mortality, and Great Horned Owls (*Bubo virginianus*; GHO) were the largest cause of nest failure for both species. A comparison of our data with other studies indicated that for many criteria, BWH and RSH were less productive in western New York than elsewhere. Reasons for this were not clear for RSH, although nest predation was an important factor. Our more extensive data for BWH explain in part their lower productivity in western New York as a function of habitat, clutch size, age of nesters, predation and reuse of nest. BWH nesting success was greater for new nests than rebuilt ones; greater for adult/adult pairs compared to adult/yearling pairs, greater in deciduous-mixed woodlands compared to conifer plantations, and greater for nests more distant from woodland openings. Three-egg clutches produced more fledglings than 2-egg clutches, but 2-egg clutches produced more fledglings per egg. We interpreted the BWH as an r-selection strategist over its lifetime, compared to many larger buteos, but the species seems capable of optimizing its reproductive effort in New York in any given year by employing brood reduction and possibly clutch adjustment reproductive strategies.

Although the natural history (Burns 1911), nesting ecology (Matray 1974), and nesting habitat (Keran 1976) of the Broad-winged Hawk (*Buteo platypterus*; BWH) have been studied, only a few studies included in-depth quantitative analysis of reproductive success (Rusch and Doerr 1972; Keran 1976; Armstrong and Euler 1982; Janik and Mosher 1982; Rosenfield 1984). There is documentation of the nesting density of the species in Wisconsin, Minnesota and Alberta (Rusch and Doerr 1972; Keran 1978; Rosenfield 1984), but not in the Northeastern United States. BWH populations appear healthy, but many researchers have suggested a general decline in Red-shouldered Hawk (*Buteo lineatus*; RSH) populations (Bent 1937; Brown 1971; Henny et al. 1973; Mason 1980; Bednarz and Dinsmore 1981), and the species appears on several state endangered and threatened species lists (i.e., Illinois, Iowa, Michigan, Minnesota, New York, Wisconsin; Anon. 1984). Bent (1937) and Stewart (1949) suggested that BWH and RSH select different nesting habitats, and Titus and Mosher (1981) and Armstrong and Euler (1982) quantified differential habitat utilization of both species. However, preliminary field work in western New York indicated that these species were locally sympatric and could be studied simultaneously.

Because the BWH's 1–4 eggs hatch asynchronously (Lyons and Mosher 1987), the species appears to be a simple brood reduction strategist (O'Connor 1977). However, Howe (1976) showed that the Common Grackle (*Quiscalus quiscula*) can combine this strategy with a resource storage strategy (see O'Connor 1977) in which eggs are provisioned with extra lipids so that young may survive short periods of food shortage. If a food shortage is lengthy, then brood reduction will occur. We looked for the presence of a second reproductive strategy in the BWH by assessing clutch size differences between years and marking and measuring eggs and monitoring the hatching sequence within clutches. Egg size/hatching sequence data will be the subject of a future paper.

Specific objectives of our study were: To document ecological nesting densities of both species; to characterize and compare breeding habitats of both; and to compare quantitatively rates of reproductive success during 2 or more breeding seasons, looking especially for nest success in relation to clutch size.

STUDY AREA

Our study area was in central and northern Chautauqua County, New York, a characteristically flat plain along Lake Erie bordered by hilly terrain a few miles from the lake. Chautauqua County is bordered by Pennsylvania to the south, Lake Erie to the northwest, and Cattaraugus County to the east. Historically, land along the lake has been used largely for grape production. Upland areas have been farmed or logged. Some farmland has returned fallow and some was used by the Civilian Conservation Corps in the 1930s for monocultural plantings of Scotch pine (*Pinus sylvestris*), red pine (*P. resinosa*) and tamarac or European larch (*Larix decidua*). Overstory was comprised of approximately 45-yr-old individuals of these species, and the understory was dominated by sugar maple (*Acer saccharum*). Much acreage resembled or was succeeding to a typical maple-beech-hemlock (*Acer-Fagus-Tsuga*) association (Shelford 1963).

Although most of the study area was forested by a maple-beech-hemlock association or a prior sere, some acreage supported oak-hickory (*Quercus-Carya* spp.) or aspen-black cherry (*Populus* spp.-*Prunus serotina*). In a few areas larch was the dominant species with sugar maple (*A. saccharum*) understory. Topography was very hilly with numerous deep ravines. Water in some form (stream, pond, swamp) was present within 0.4 km of all the study sites.

The principal study site was the New York State Canadaway Creek Wildlife Management Area (approximately 875 ha) and adjoining land, a broad, deeply dissected upland plateau predominantly covered with deciduous forest, but also with conifer plantings. The area is managed primarily to ensure quality habitat for wildlife, especially game species, and secondarily is available for recreational use.

METHODS

This study was conducted from 1978 through 1980. Thorough ground censuses for old stick nests were conducted during late winter and early spring before nesting hawks returned. All old nest sites were revisited after hawks returned, and other areas where BWH and RSH were observed were also censused.

Nests being used (active) were revisited approximately once/wk until hatching to document clutch size and egg survival. Use of a pole and mirror device (Parker 1972) minimized nest disturbance. Eggs were measured and weighed approximately 1 wk prior to hatching. Nest height (measured using the pole and mirror device or carefully estimated from sightings on a person of known height standing at the tree base), distance of nest tree from a roadway or woodland opening (measured by pacing), and the number of limbs supporting a nest were also recorded. Once eggs hatched, nests were visited every 2–4 d and nestlings were marked, weighed, and measured. Culmen, tarsal length, and lengths of the sixth primary (conventional numbering) of the right wing and the right central rectrice were measured. Young were banded with U S Fish and Wildlife Service bands prior to fledgling. In 1979 plumages of breeding Broad-wings were used as a basis for age determination. Naphthalene crystals were placed at the base of active nest trees to deter terrestrial predators. Addled eggs and prey remains were collected at nests whenever possible, and behavior of the nesting hawks was observed. Predation was detected by observing Great Horned Owls (*Bubo virginianus,* GHO) near nests, presence of GHO feathers in nests, or at 1 nest noticing the strong odor of Striped Skunk (*Mephitis mephitis*) in the nest (Striped Skunks are not known to climb trees [R. Cole pers. comm.] and GHO often prey on Striped Skunks).

Nestlings were aged by observing hatching dates. Statistical analyses followed Sokal and Rohlf (1969).

RESULTS

Nesting Habitat. Both BWH and RSH nested in approximately the same type of upland woods, but with specific differences in nest sites. Each species used a variety of tree species, but each showed a preference (Table 1). BWH used larch (*Larix decidua*) most often (33%), whereas RSH apparently preferred American beech (*Fagus grandifolia* 39%). BWH showed a tendency to nest on slopes, but RSH chose relatively level terrain. Both species nested <1 km from streams, ponds, or swamps. BWH seemed to nest closer to woodland openings (road cuts, field, etc.) and lower in trees than RSH, respectively: 90 ± 54 m [N = 17] versus 182 ± 164 m [N = 6]; and, 11.8 ± 3.2 m [N = 18] versus 13.4 ± 2.4 m [N = 11], although neither comparison was statistically significant (distance to woodland opening F = 2.15, P > 0.1, single classification analysis of variance (ANOVA) and nest height F = 1.85, P > 0.1, ANOVA). Both species seemed to prefer the first substantial crotch in a tree except in larch where nests were placed on a platform of horizontal branches against the trunk, and both used approximately the same number of limbs for nest support (BWH, 4.3 ± 1.1 [N = 16] and RSH, 4.2 ± 0.7 [N = 12]).

Nesting Density. We could measure ecological density only on the 1200 ha of the Canadaway Creek Wildlife Management Area and adjoining private land. In 1978, 6 RSH pairs and 5 BWH pairs were found. Additionally, we suspected the presence of 1 additional pair of each species based on sightings

Table 1. Species of trees used for nest sites by Broad-winged and Red-shouldered Hawks in western New York. Only active nests were counted.

Tree Species	Frequency of Use: Broad-wing	Frequency of Use: Red-shoulder
Scotch Pine (*Pinus sylvestris*)	1	0
European Larch (*Larix decidua*)	6	1
Quaking Aspen (*Populus tremuloides*)	1	1
Yellow Birch (*Betula alleghaniensis*)	1	2
American Beech (*Fagus grandifolia*)	0	7
Northern Red Oak (*Quercus rubra*)	2	0
Sweet Crab Apple (*Malus coronaria*)	1	0
Black Cherry (*Prunus serotina*)	3	1
Sugar Maple (*Acer saccharum*)	2	0
Red Maple (*Acer rubrum*)	0	2
Maple sp. (*Acer* sp.)	0	2
American Basswood (*Tilia americana*)	1	0
White Ash (*Fraxinus americana*)	0	2
Total number of tree species	9	8
Total nests	18	18

Table 2. Raptor species occurring in the 1200 ha Canadaway Creek Wildlife Management Area and adjacent woodlands and probable densities in 1978.

Species	Occurrence
Cathartes aura	1 or 2 pairs
Circus cyaneus	1 pair
Accipiter striatus	1 pair
Buteo jamaicensis	1 pair
Buteo lineatus	6 or 7 pairs
Buteo platypterus	5 or 6 pairs
Falco sparverius	1 pair
Asio otus	1 pair
Bubo virginianus	1 pair
Strix varia	1 pair

and calls of hawks. Including suspected pairs, nesting densities of RSH and BWH were 1 pair/171 ha and 1 pair/200 ha, respectively, of forested land. BWH and RSH more often nested adjacent to each other than to conspecifics. Nearest neighbor distances were 877 ± 422 m (N = 12) for BWH/RSH, 1441 ± 331 (N = 11) for BWH/BWH, and 1271 ± 640 (N = 4) for RSH/RSH. A single active Barred Owl (*Strix varia*) nest was 120 m from a RSH nest and 578 m from a BWH nest.

Several other species of raptors were present during the breeding season in the Canadaway Creek area (Crocoll and Parker 1986; Table 2) but were not carefully censused, and some nesting pairs were probably overlooked. Nevertheless, overall raptor density was conservatively estimated at 1 pair/63.2 ha.

Nesting Chronology. BWH. Broad-winged Hawks were first seen on the study area on 12 April in 1978, on 23 April in 1979, and on 19 April in 1980. These were probably local breeding birds because active nests were subsequently found near sightings. Migrant BWHs were also observed in the study area in April. Nest building or rebuilding began soon after occupying nesting territories. Active nests were verified by the presence of green sprigs or down, or a bird on the nest. Nests were found as early as 24 April, and partially constructed nests were found as late as 14 May, suggesting a nest construction period of approximately 3 wks. Backdating from hatching dates, and assuming 30 days for incubation as did Matray (1974), egg laying occurred mainly during the second and third wks of May.

Eleven of 12 BWH eggs hatched in the first 2 wks of June (Fig. 1). Variation in hatching date seemed unrelated to year or clutch size. Mean first egg hatching dates for 1978, 1979, and 1980 were 16 June, 7 June, and 10 June, respectively. Mean first egg hatching date for the 3-yr period was 10 June.

Average interval ($\bar{x}$ ± S.D.) between any 2 eggs hatching for any size clutch was 1.87 ± 1.36 d (N = 31). Eggs hatched 1 d apart (N = 4) in all 2-egg clutches (N = 4). In 3-egg clutches the average time between any 2 eggs hatching was 2.00 ± 1.41 d (N = 24). The second egg hatched an average of 0.38 ± 0.52 d (N = 8) after the first, and the third egg hatched an average of 2.62 ± 0.74 d (N = 8) after the second. In a single 4-egg clutch, the second egg hatched <24 hr after the first, the third egg failed to hatch, and the fourth hatched 3 d after the second.

First flights of nestlings, usually in response to disturbance, occurred at 31.4 d of age ($\bar{X}$; N = 11, range 29–39). There was little variation in the age of first flight among individuals from broods of different sizes. In this study fledging was defined as the ability of an individual to sustain horizontal flight and occurred when the nestlings were 5–6 wks old.

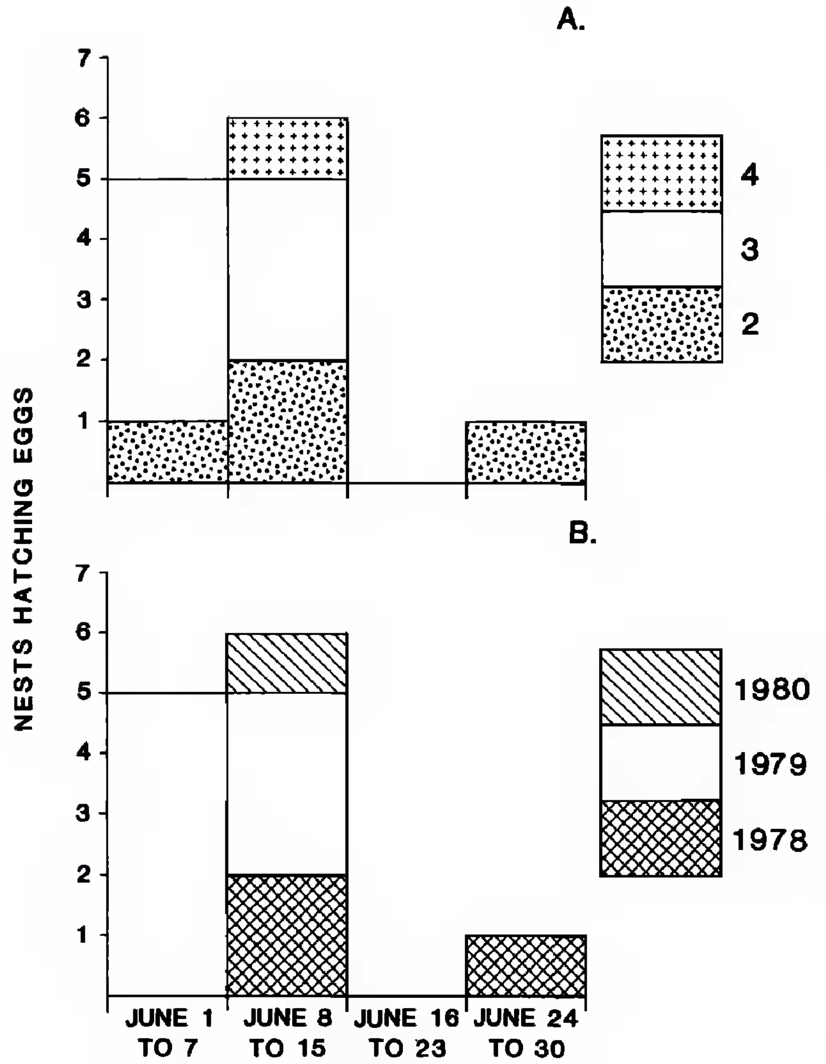

Figure 1. Hatching dates for the first egg in clutches of Broad-winged Hawks. The numbers show clutch sizes in A and years in B.

Earliest fledging date was 4 July and the latest was 2 August. Most young (88.9%) fledged during the second and third wks of July. BWH were last seen on the study area on 5 September in 1978 and on 3 September in 1979.

RSH. Twenty active RSH nests were found during our 3-yr study but were intensively studied only during 1979. The following schedule was constructed primarily from data obtained in 1979.

RSH were first seen during the second and third wks of March when nest relining was also observed. Adults were sitting on nests as early as the first wk in April and may have been incubating eggs. Most eggs hatched during the second and third wks of May, which suggests a minimum incubation period of 4–5 wks in western New York. Fledging occurred during the third and fourth wks of June, with the exception of 1 nest at which a single young fledged on 11 July, suggesting a nestling period of approximately 5 wks.

Reproductive output and nest success were analyzed for each of 3 time periods. The egg period encompassed the time from laying of the first egg until its hatching, the nestling period was the time from the hatching of the first egg until the fledging of the first young, and the fledging period was the time from the fledging of the first young until migratory departure.

In most respects the BWH seemed more successful in 1979 than in 1978 (Table 3), but sample sizes were small and statistical significance could seldom be shown. Clutch size was significantly larger ($F = 4.92$, $P < 0.05$, ANOVA) in 1979 than 1978. Most notably, overall productivity of the fledglings per nesting attempt in 1979 was nearly twice that of 1978.

Ten of 18 BWH nesting attempts suffered some mortality. Total nest loss occurred more often during the egg period in both years, but only for 1979 was the difference statistically significant ($t_s = 1.96$, $P < 0.05$, arcsine test). In 1979 more nests hatching eggs survived the nestling period than in 1978 ($t_s = 1.71$, $P < 0.05$). In 1979 the overall percentage of successful nests seemed higher than 1978, but the difference was not statistically significant ($t_s = 1.25$, $P \sim 0.10$).

Because records for some RSH nests are incomplete, only limited generalizations are possible. RSH clutch size was larger than BWH (Table 3), but RSH fledged fewer young, which probably reflects largely the lower hatching success for RSH. A third egg which failed to hatch was suspected for two 2-egg clutches because of the presence of egg shell fragments beneath the nest early in the egg period. Therefore, data presented in Table 3 represents the minimum percentage of eggs hatched. Discounting the observed shell fragments would have resulted in a hatching percentage of 77%. Rates of nest success for RSH and BWH were similar during the egg period, but BWH nests seemed more successful during the nestling period.

Success and Clutch Size. Only 1 BWH clutch each of 1 egg and 4 eggs was found. Therefore, comparisons of success (Table 4) were made only between clutches that were originally of 2 or 3 eggs. The average number of fledglings per nest was not statistically greater with larger clutch size, but a larger sample size might well establish statistical significance. Two-egg clutches produced more fledglings/egg hatched than did 3-egg clutches ($t = 2.45$, $P < 0.01$), but a similar comparison for fledglings/egg laid was not statistically significant. Percentages

Table 3. Productivity and nest success of Broad-winged and Red-shouldered Hawks in western New York. Sample sizes are in parentheses.

PARAMETER	BROAD-WINGED HAWK 1978	BROAD-WINGED HAWK 1979	BROAD-WINGED HAWK TOTAL	RED-SHOULDERED HAWK ALL YEARS
Total nests found	6	10	18[a]	9
Average clutch size	2.00 ± 0.82 (4)	2.89 ± 0.60 (9)	2.60 ± 1.09 (15)[a]	3.00 ± 1.00 (5)
Average no. of eggs hatching	1.40 ± 1.34 (5)	2.30 ± 1.25 (10)	1.88 ± 1.32 (17)[a]	2.00 ± 1.58 (5)
Percentage of eggs hatching	90.9 (11)	88.5 (26)	83.3 (42)[a]	66.7 (15)
Percentage of fledglings per egg laid	75.0 (8)	73.1 (26)	69.2 (39)[a]	—
Percentage of fledglings per egg hatched	85.7 (7)	82.6 (23)	84.4 (32)[a]	—
Avg. fledglings per nest	1.00 ± 1.10 (6)	1.90 ± 1.20 (10)	1.50 ± 1.20 (18)[a]	1.11 ± 1.17 (9)
Avg. fledglings per successful nest	2.00 ± 0 (3)	2.38 ± 0.74 (8)	2.25 ± 0.62 (12)[a]	2.00 ± 0.71 (5)
% Nests successful in:				
Egg period	66.7 (6)	80.0 (10)	72.2 (18)[a]	75.0 (8)
Nestling period	75.0 (4)	100 (8)	92.3 (13)[a]	83.3 (6)
Overall	50.0 (6)	80.0 (10)	66.7 (18)[a]	55.6 (9)

[a] Total includes 2 nests found in 1980.

of successful nests in both the egg and nestling periods were very similar between 2-egg and 3-egg clutches.

Success and Age of BWH. BWH yearlings were first observed paired and breeding with adults in 1979. Age of both parents was known for only 1 pair in 1978 and 1980. All breeding yearlings were males. Adult/adult pairs were more successful than adult/yearling pairs for most criteria in Table 5. However, only the percentage of eggs hatching showed a significant difference ($t_s = 2.31$, $P \simeq 0.01$) favoring the adult/yearling pairs. Clutch size of 1 mixed pair was unknown and was excluded from some of the calculations.

Success and Reuse of Nests by Broad-wings. Of fifteen BWH nests of known age, 5 (33%) had been rebuilt (Table 6). Clutch size was not statistically different between the 2 ages of nests, but nest success appeared greater in all criteria for newly constructed nests compared to reused nests, although

Table 4. Productivity of different clutch sizes[a] in the Broad-winged Hawk in western New York. Sample sizes are in parentheses.

	CLUTCH SIZE 1	CLUTCH SIZE 2	CLUTCH SIZE 3	CLUTCH SIZE 4
Number of nests	1	5	8	1
Average No. of eggs hatching	0 (1)	1.60 ± 0.89 (5)	2.62 ± 1.06 (8)	3.00 (1)
Percentage of eggs hatching	0 (1)	80.0 (10)	87.5 (24)	75.0 (4)
Percentage of fledglings per egg laid	0 (1)	80.0 (10)	66.7 (24)	75.0 (4)
Percentage of fledglings per egg hatched	—	100 (8)	76.2 (21)	100 (3)
Average fledglings per nest	0 (1)	1.60 ± 0.89 (5)	2.00 ± 1.06 (8)	3.00 (1)
Average fledglings per successful nest	—	2.00 ± 0 (4)	2.28 ± 0.76 (7)	3.00 (1)
% Nests successful in:				
Egg period	0 (1)	80.0 (5)	87.5 (8)	100 (1)
Nestling period	—	100 (4)	100 (7)	100 (1)
Overall	0 (1)	80 (5)	87.5 (8)	100 (1)

[a] Clutch size was not determined at 2 nests and one pair did not lay eggs.

Table 5. Reproductive output and nest success by age composition of pairs of breeding Broad-winged Hawks. Sample sizes in parentheses.

	PAIR COMPOSITION	
	ADULT/ADULT	ADULT/SUBADULT
Total number of nests	6	4
Average clutch size	3.00 ± 0.63 (6)	2.67 ± 0.58 (3)
Average No. of eggs hatching	2.33 ± 1.21 (6)	2.00 ± 1.41 (4)
Percentage of eggs hatching	77.8 (18)	100 (8)
Percentage of fledglings per egg laid	72.2 (18)	75.0 (8)
Percentage of fledglings per egg hatched	92.9 (14)	75.0 (8)
Average fledglings per nest	2.17 ± 1.17 (6)	1.50 ± 1.39 (4)
Average fledglings per successful nest	2.60 ± 0.55 (5)	2.00 ± 1.00 (3)
% Nests successful in:		
Egg period	83.3 (6)	75.0 (4)
Nestling period	100 (5)	100 (3)
Overall	83.3 (6)	75.0 (4)

the difference showed statistical significance only in the cases of percentage of eggs hatching ($t_s = 2.22$, $P < 0.05$) and percentage of fledglings/egg laid ($t_s = 2.27$, $P < 0.05$).

Success and BWH Nest Sites. Fledging success of BWH was not related to the number of limbs supporting nests ($F_s = 0.62$, $P > 0.5$, ANOVA) or nest elevation ($F_s = 0.81$, $P > 0.25$, ANOVA) (Fig. 2A and 2B). A trend toward increased success was indicated for nests farther from woodland openings but was not statistically significant ($F_s = 2.1$, $P > 0.1$, ANOVA; Fig. 2C).

Essentially, BWH nested in 2 habitat types: deciduous mixed woodland, and small-stand conifer plantations (approximately 1 ha) contiguous with beech-maple-hemlock forest. Average clutch size and average number of fledglings/nest were similar between different habitats (Table 7). However, approximately 1 less egg/nest hatched from nests in conifer plantations than from those in the mixed deciduous-conifer habitat, apparently the result of greater loss of nests in plantations during the egg period ($t_s = 1.59$, $P \simeq 0.06$). A larger percentage of eggs hatching in deciduous mixed habitat as compared with plantations ($t_s = 2.72$, $P < 0.01$) was associated with a higher percentage of fledglings/

Table 6. Nest success of new versus rebuilt Broad-winged Hawk nests in western New York. Sample sizes in parentheses.

	NEW NESTS	REBUILT NESTS
Total number of nests	10	5
Average clutch size	2.44 ± 1.13 (9)	2.40 ± 0.39 (5)
Average No. of eggs hatching	2.10 ± 1.20 (10)	1.60 ± 1.52 (5)
Percentage of eggs hatching	95.4 (22)	66.7 (12)
Percentage of fledglings per egg laid	86.4 (22)	50.0 (12)
Percentage of fledglings per egg hatched	90.5 (21)	75.0 (8)
Average fledglings per nest	1.90 ± 1.00 (10)	1.20 ± 1.30 (5)
Average fledglings per successful nest	2.38 ± 0.52 (8)	2.00 ± 1.00 (3)
% Nests successful in:		
Egg period	80.0 (10)	60.0 (5)
Nestling period	100 (8)	100 (3)
Overall	80.0 (10)	60.0 (3)

egg laid, although the only nest that failed during the nestling period was in mixed habitat. Percentage of successful nests was essentially the same during the egg and nestling periods in the mixed habitat, but a greater percentage of nests failed in the egg period than in the nestling period in conifer plantations ($t_s = 2.28$, $P < 0.05$).

Mortality Factors. Four mortality factors reduced BWH reproductive success. Nest desertion caused only the loss of 1 egg and 1 nest attempt, and egg failure was known to cause only the loss of 1 egg. Predation accounted for half the loss of Broad-wing nests (5 of 10), and most occurred prior to hatching. Five eggs and 4 nestlings were known to be lost to predators, and GHO were judged responsible at 4 nests. During the 3 yrs of the study, 4 adults were killed by predators, all at different nests, and 3 of those by GHO (see Methods). The remaining adult died from an unknown cause. Four yearlings were recruited into the breeding population in 1979, indicating that at least 3 additional adults in the local population probably suffered some form of mortality prior to the breeding season. Starvation was secondary to predation by causing the loss of 4 nestlings (2 in 1 nest, 1 in each of 2 others).

RSH mortality showed a roughly similar pattern. Predation eliminated 3 nests (1 egg, 1 nestling known lost). Starvation impacted 2 nesting attempts (3 nestlings at 2 nests) but resulted in no complete nest failures. It was not possible to determine if predation on Red-shoulder nests was more prevalent during the egg period than the nestling period, but Great Horned Owls were the responsible predator in all cases judging by the presence of feathers and other observations similar to failed BWH nests.

Food Habits. BWH in Chautauqua County, New York were generalized predators bringing at least 14 species of vertebrates to nests (Table 8). Because invertebrate remains were rarely found in the nests, their importance in the BWH diet is unclear. Clearly, mammals (chipmunks, moles, shrews) and miscellaneous birds predominated, but toads and garter snakes were taken also. The percent composition of different vertebrates in the Broad-wing's diet changed considerably between 1978 and 1979 with the greatest shift being to birds. Of 20 prey items found in 1978, 12 (60%) were mammals, 4 (20%) were reptiles, and only 2 each (10%) were birds and amphibians. In 1979, 14 (33%) of 42 prey items were birds, mammals fell to 40% (17), while reptiles and amphibians 4 (10%) and 7 (17%), respectively, remained uncommon. In 1978 an average of 0.35 vertebrate prey items were found during each nest visit (N = 57) in comparison to 0.54 prey items found per visit (N = 78) in 1979. Prey items [2 Eastern Chipmunks; 1 Shorttail Shrew; 1 Masked Shrew (*Sorex cinereus*)] were found at only 2 RSH nests.

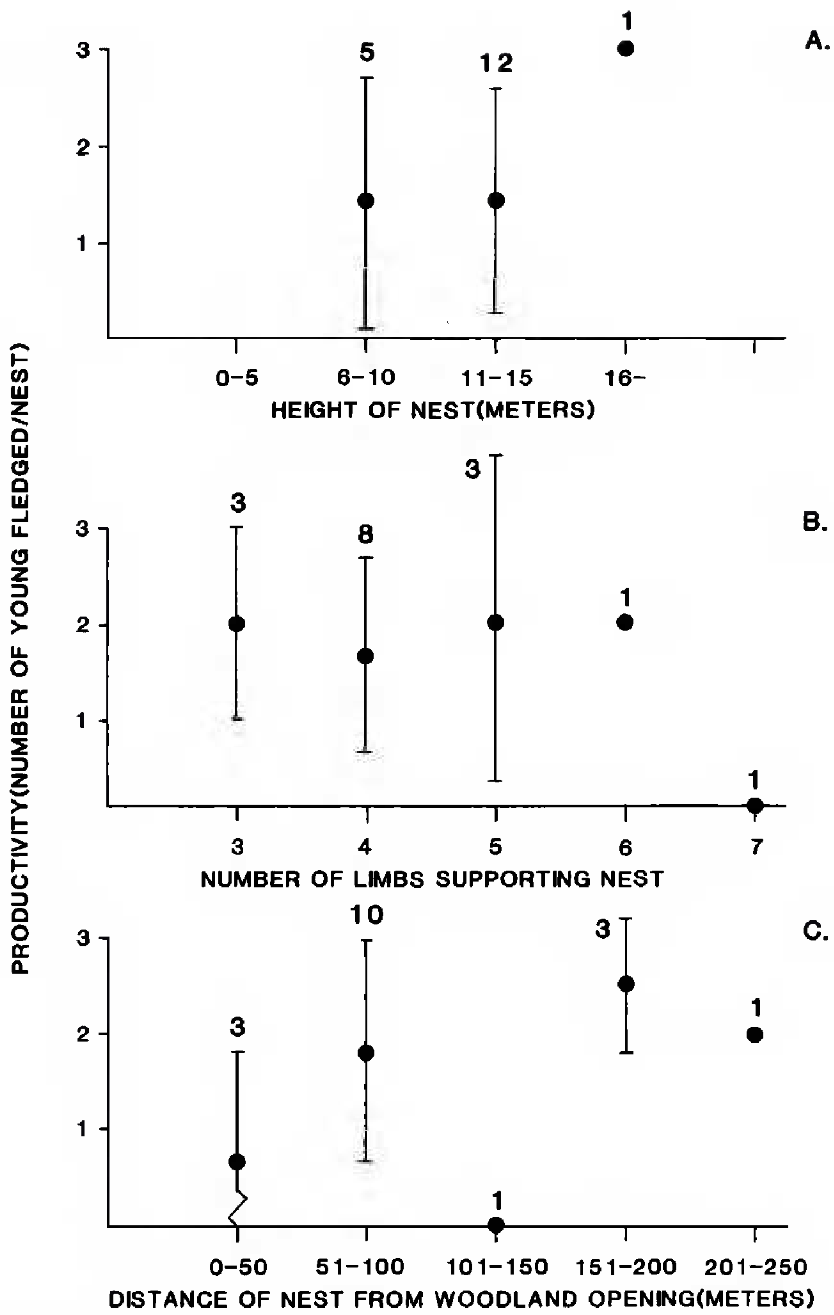

Figure 2. Production of BWH fledglings associated with A, nest height; B, number of supporting limbs, and C, distance of nest from a woodland opening. Each point represents the mean and the bars represent the S.D. Nest sample size appears above each bar.

DISCUSSION

Nesting Characteristics and Densities of BWH and RSH. BWH. In most parts of its range, BWH associates with dense forests (Burns 1911; Bent 1937). However, forest type is quite variable [e.g., maple-beech-hemlock in this study, oak-aspen in Wisconsin-Minnesota (Keran 1978), hemlock-yellow birch

Table 7. Reproductive success of Broad-winged Hawks in two habitat types in western New York. Sample sizes in parentheses.

	DECIDUOUS MIXED WOODLANDS	CONIFER PLANTATIONS
Total number of nests	11	7
Average clutch size	2.56 ± 1.13 (9)	2.28 ± 0.76 (7)
Average No. of eggs hatching	2.44 ± 1.01 (9)	1.43 ± 1.40 (7)
Percentage of eggs hatching	95.6 (23)	62.5 (16)
Percentage of fledglings per egg laid	73.9 (23)	62.5 (16)
Percentage of fledglings per egg hatched	77.3 (22)	100 (10)
Average fledglings per nest	1.54 ± 1.13 (11)	1.43 ± 1.40 (7)
Average fledglings per successful nest	2.12 ± 0.64 (8)	2.50 ± 0.58 (4)
% Nests successful in:		
Egg period	90.0 (10)	57.1 (7)
Nestling period	88.9 (9)	100 (4)
Overall	80.0 (10)	57.1 (7)

in the Adirondack Mountains (Matray 1974)]. Only in this study has BWH been observed nesting in conifer plantations. Other studies reported nesting close to some type of forest opening (Table 9), but BWH in western New York unaccountably nested farther from forest openings than other populations. Nest heights appeared to be similar among different regions except for Wisconsin where nests were substantially lower (Keran 1978). Clearly, BWH displays a degree of adaptability in choice of nesting habitat, but no detailed patterns are apparent.

Few comparative data exist on BWH nesting densities. Rusch and Doerr (1972) reported about 1 pair/23.3 km^2, which is much less dense than the Chautauqua study area (approximately 1 pair/2 km^2), probably because the Alberta study site was on the western edge of the species' range. Keran (1978) and Rosenfield (1984) reported breeding densities of 1 pair/5.2 km^2 and 1 pair/2.4 km^2, respectively, for Minnesota and Wisconsin. In Chautauqua County the BWH appeared subjectively to be about the third or fourth most common raptor, behind RSH and Red-tailed Hawks (*Buteo jamaicensis*) and possibly GHO.

We know of only 3 other studies that reported on densities of raptor communities: Craighead and Craighead (1956) in Michigan (1 pair/144.7 ha), Brown (1966) in Kenya (1 pair/84 ha), and U.S.D.I. (1979) in the Snake River Birds of Prey study area, Idaho (1 pair/91.7 ha). Clearly, total raptor density in the Canadaway Creek (1 pair/63.2 ha) ranks with others as a very dense raptor community, whether or not birds forage outside the study area (as do the birds at Snake River).

Breeding schedule of BWH in western New York seems to coincide most closely with Wisconsin-Minnesota (Keran 1976) and the central Appalachians (Janik and Mosher 1982). Egg laying and hatching occurred from early May to early June and fledging from mid to late July in both the Wisconsin-Minnesota and central Appalachian populations.

RSH. Although several studies (Stewart 1949; Wiley 1975; Preston et al. 1989) indicate an association between Red-shouldered Hawk nesting and low floodplain forests, only 1 of our 20 active RSH nests was in floodplain forest. Most were in upland hills, but all were close to some form of surface water which is in agreement with other studies. Forest habitat used by RSH in this study was most similar to that used by populations in the Waterloo region of Ontario (Sharp and Campbell 1982) and in southwestern Quebec (Morris et al. 1982). The Canadian studies as well as Titus and Mosher (1987) also indicated preference for the American beech as a nest tree.

A comparison of several studies (Table 10) suggests that RSH use nest sites with similar characteristics throughout much of their geographic range However, few estimates of nesting densities are available. Craighead and Craighead (1956) computed only crude density for an entire township, which included unsuitable cropland as well as suitable woodland habitat. Consequently, their nesting density is not directly comparable to western New

York. Stewart (1949) documented a nesting density in central Maryland that was very similar to western New York even though habitats were much different. In central Maryland, RSH nested only in low river floodplains where the only other nesting raptor was the Barred Owl.

Interestingly, the RSH was the most common nesting raptor in Chautauqua County during the study despite the fact that numbers appear to be declining in many parts of the range (Crocoll and Parker 1988). Most studies (Bednarz and Dinsmore 1981; Kimmel and Fredrickson 1981; Sharp and Campbell 1982) indicate that the primary cause of decline is loss of extensive forested habitat. Currently, habitat does not appear to be limiting in western New York (Crocoll and Parker, pers. obs.) and may in fact be increasing due to a reversion of farm land and old timber harvest areas to woodlands.

Several other studies have reported on RSH nesting chronology (Craighead and Craighead 1956; Henny et al. 1973; Wiley 1975; Portnoy and Dodge 1979; Kimmel and Fredrickson 1981). Chronology in Michigan (Craighead and Craighead 1956) was more similar to western New York than other areas, where some showed earlier (Henny et al. 1973; Wiley 1975; Kimmel and Fredrickson 1981) and some later (Portnoy and Dodge 1979) schedules.

Other studies (Stewart 1949; Titus and Mosher 1981) indicated that BWH and RSH do not usually nest in close proximity. However, we found the opposite true in western New York as did Armstrong and Euler (1982) in central Ontario. Though the general nesting habitats of each species are similar, there probably exist subtle habitat differences similar to those reported in Titus and Mosher (1981), such as distance to nearest forest opening, topography, tree density, ground cover, and percent coniferous trees (Armstrong and Euler 1982) that help reduce potential competition for nest sites. Also, as Fuller (1979) suggested, two species may use overlapping home ranges at different times of the day or week to reduce potential competition for space.

Comparative Reproductive Success of Different BWH and RSH Populations. BWH. Table 11 presents reproductive data for BWH populations from 6 studies. They permit few statistical comparisons and only one comparison among all six populations (% nests successful overall). Only for the population in western New York has the relationship between habitat, age of nesters, clutch size, nest reuse, productivity, and reproductive success been reported. Some measures of productivity were roughly similar among different populations, but the western New York population with a high average clutch size had one of the lowest average numbers of young fledged per nest. This study area also seems to have the lowest percentage of successful nests, although the difference was not statistically significant. Lower success in western New York was at least partly due to the statistically lower success of nests in the egg period ($G = 7.44$, $P < 0.025$ R x C test of independence).

Surprisingly, causes of mortality and nest failure have received attention in only 1 other study (Ro-

Table 8. Food items in 13 Broad-winged Hawk nests 1978–1980 in Chautauqua County, New York.

SPECIES	N	% OCCURRENCE
Mammals		
Blarina brevicauda	9	13.0
Condylura cristata	6	8.7
Parascalops breweri	2	3.0
Tamias striatus	10	14.5
Microtus pennsylvanicus	2	3.0
Unidentified	3	4.3
Total mammals	32	46.4
Birds		
Colaptes auratus	2	3.0
Cyanocitta cristata	3	4.3
Bombycilla cedrorum	1	1.4
Junco hyemalis	2	3.0
Unidentified	10	14.5
Total birds	18	26.1
Reptiles		
Storeria dekayi	1	1.4
S. occipitomaculata	1	1.4
Thamnophis sirtalis	5	7.2
Unidentified	2	3.0
Total reptiles	9	13.0
Amphibians		
Bufo americanus	7	10.1
Rana pipiens	2	3.0
Total amphibians	9	13.0
Unidentified vertebrate	1	1.4
Total vertebrates	69	100
Invertebrates		
Crustacea (Crayfish)	2	?
Insecta (grasshoppers and caterpillars)	?	?

Table 9. Nesting habitat characteristics of several Broad-winged Hawk populations. Sample size in parentheses.

	Nest Height (m)	No. Support Limbs	Distance to Forest Opening (m)
Wisconsin-Minnesota (Keran 1978)	—	3.8 ± 0.4	42
Central Appalachians (Titus and Mosher 1981)	13.7 ± 3.0 (24)	—	63 ± 61 (24)
Western New York (this study)	11.8 ± 3.2 (18)	4.3 ± 1.1	90 ± 54 (17)
Adirondack Mountains, NY (Matray 1974)	13.3 ± 1.36 (14)	—	—
Wisconsin (Rosenfield 1984)	8.2 ± 2.7 (72)	—	—
Central Ontario (Armstrong and Euler 1982)	11.8 ± 2.8 (27)	—	42.1 ± 30.2 (27)

senfield 1984) which reported that almost twice as many eggs as nestlings were lost, concluding that major impacts occurred during the egg period, as we observed. Rosenfield (1984) also observed the same types of mortality, except starvation of nestlings was not detected. He did record a significantly higher incidence of eggs that failed to hatch (9.1%) compared to our western New York study (2.4%) (t_s = 1 75, P ≃ 0.04 arcsine transformation, test of equality of 2 percentages) and suspected that predation was due to Raccoon (*Procyon lotor*) and American Crow (*Corvus brachyrhynchos*). Ours is the first study to report predation by GHO, which clearly can have a substantial impact on a local BWH population (also see Parker 1974).

Several raptors are known to reuse nests (Brown and Amadon 1968). Rosenfield (1984) reported reuse of nests both in the year after and 2 yrs after construction. To reuse nests is probably energetically more advantageous than building anew (Weeks 1978). In addition nest reuse is most likely to occur if the nest was successful the previous year (Craighead and Craighead 1956). In our study, however, reuse only occurred 2 yrs after construction and most often in pine plantations. In fact, reused nests in New York were less successful than new ones, nests further from woodland openings appeared more productive than nests relatively close to openings (Fig. 2), and reused nests were much closer to openings than newly constructed nests. We suggest reuse of a nest, placement nearer open areas, or both increases the likelihood of nests being noticed by GHO One possible pressure for nest reuse in pine plantations was the lack of suitable nest trees (Crocoll and Parker, pers. obs.).

Although *Buteo* species usually start breeding at 2 or 3 yrs (Newton 1977) in adult plumage, there have been some reports of breeding subadults (Red-

Table 10. Red-shouldered Hawk nest site characteristics. Sample size in parentheses.

	Nest Height (m)	No. Supporting Limbs	Distance To Forest Opening (m)	Breeding Density
Western New York (this study)	13.4 ± 2.6 (11)	4.2 ± 0.7 (12)	182 ± 164 (6)	1 pair/171 ha
Southwest Quebec (Morris, et al. 1982)	14.0 ± 3.6 (54)	4.2 (54)	—	—
Waterloo Region (Sharp and Campbell 1982)	14 (9)	—	—	—
Missouri (Kimmel and Fredrickson 1981)	14.4 ± 3.6 (14)	—	—	—
Iowa (Bednarz and Dinsmore 1982)	19.1 ± 4.8 (11)	3.6 ± 0.5 (11)	—	—
Massachusetts (Portnoy and Dodge 1979)	12.0 ± 1.7 (12)	—	—	—
Central Appalachians (Titus and Mosher 1981)	13.4 ± 3.0 (10)	—		—
Central Maryland (Stewart 1949)	15 (57)	—	180 ± 141 (10)	1 pair/48.7 ha
Michigan (Craighead and Craighead 1956)	—	—	—	1 pair/645 ha
Central Ontario (Armstrong and Euler 1982)	14.0 ± 3.6 (9)	—	— 27.8 ± 18.2 (9)	—
Arkansas (Preston et al. 1989)	—	—	173.3 ± 73.1 (19)	—

Table 11. Comparison of Broad-winged Hawk reproductive output among 6 populations. Sample sizes in parentheses

	Central Ontario (Armstrong and Euler 1982)	Alberta, Canada (Rusch and Doerr 1972)	Minnesota and Wisconsin (Keran 1976)	Chautauqua County, NY (This Study)	Central Appalachians (Janik and Mosher 1982)	Wisconsin (Rosenfield 1984)
Total nests found	16	5	12	18	36	72
Average clutch size	—	2.40 ± 0.55 (5)	2.17 ± 0.39 (12)	2.60 ± 1.09 (15)	2.7 (15)	2.36 (70)
Average no. of eggs hatching	—	2.40 ± 0.55 (5)	2.00 ± 0.60 (12)	1.88 ± 1.32 (17)	2.1 (29)	1.81 (70)
Percentage of eggs hatching	—	100 (12)	92.3 (26)	83.3 (42)	—	77.0 (165)
Percentage of fledglings per egg laid	—	83.3 (12)	84.6 (26)	69.2 (39)	—	64.8 (165)
Percentage of fledglings per egg hatched	—	83.3 (12)	91.7 (24)	84.4 (32)	—	84.3 (127)
Average fledglings per nest	1.5	2.00 (5)	1.83 ± 0.83 (12)	1.50 ± 1.20 (18)	1.74 (34)	1.53 (70)
Average fledglings per successful nest	1.7	2.00 (5)	2.00 ± 0.63 (11)	2.25 ± 0.62 (12)	1.90 (31)	1.94 (55)
% Nests successful:						
Egg period	—	100 (5)	100 (12)	72.2 (18)	—	—
Nestling period	—	100 (5)	91.7 (12)	92.3 (13)	—	—
Overall	87.5 (16)	100 (5)	91.7 (12)	66.7 (18)	86.1 (36)	78.6 (70)

tailed Hawks, Luttich et al. 1971; and Red-shouldered Hawks, Henny et al. 1973; Wiley 1975; Apanius 1977). Yearling Broad-wings have not previously been reported to nest (Newton 1979).

In general young breeders are not as successful as older individuals (Lack 1968; Fisher 1975; Brown 1978). Additionally, Crawford (1977) indicated that subadult female Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) nested in lower quality territories than adults. In our study, BWH pairs that included subadults were apparently less successful than adult/adult pairs (Table 5) even though the former used the habitat (mixed deciduous coniferous forest) producing more young per nest and greater nest success (Table 7).

Male BWH provide all the food during incubation and the early nestling period (Matray 1974). Therefore, mixed pairs in which the male is the subadult should be most successful in years of high food abundance when inexperienced breeding males would have a better chance of obtaining sufficient food.

Subadult breeders of many species start nesting later in the season than more experienced breeders [Laysan Albatross (*Diomedia immutabilis*), Fisher 1975; European Sparrowhawk (*Accipiter nisus*), Newton 1976; Great Horned Owl, McInvaille and Keith 1974]. However, in our study mixed pairs did not breed later in the season than adult/adult pairs, and overall the population in western New York appeared to breed synchronously, as do BWH in the Adirondacks (Matray 1974).

Several studies showed that nesting habitat has an effect on the nesting success of raptors (Howell et al. 1978; Newton 1976). In western New York, mixed deciduous woodlands were apparently superior to conifer plantations for BWH breeding (Table 7), even though the difference in reproductive success was not large. This situation may be explained (at least in part) by a combination of several factors. First, 67% of the rebuilt nests were found in pine plantations, and reused nests were less productive than new nests. Second, a positive (though statistically non-significant) relationship exists between nest success and distance of nest from a woodland opening (Fig. 2C), and nests in mixed deciduous woodlands were farther from a woodland opening than nests in pine plantations (92.6 m and 85.7 m, respectively). However, mixed pairs were in deciduous-mixed

Table 12. Comparison of Red-shouldered Hawk reproductive output among different populations. Sample sizes in parentheses.

	Total Nests Found	Average Clutch Size	Average No. of Eggs Hatching	Average Fledglings per Nest	Average Fledglings per Successful Nest	% Nests Successful
California (Wiley 1975)	29	2.69 ± 0.54 (29)	2.07 ± 1.03	1.34 ± 1.14 (29)	2.05 (19)	65.5 (19)
Iowa (Bednarz 1979)	8	—	2.9 (8)	2.9 (8)	3.3 ± 0.76 (8)	87.5 (8)
Michigan (Craighead and Craighead 1956)	40	3.42 (40)	2.55 (40)	1.77 (40)	—	—
Missouri (Kimmel and Fredrickson 1981)	9	—	—	2.56 ± 0.53 (9)	2.56 ± 0.53 (9)	100 (9)
New York (this study)	9	3.00 ± 1.00 (5)	2.00 ± 1.58 (5)	1.11 ± 1.17 (9)	2.00 ± 0.71 (5)	55.6 (9)
Maryland—western (Janik and Mosher 1982)	17	3.1 (6)	2.4 (8)	1.8 (10)	—	52.9 (9)
Maryland—central (Henny et al. 1973)	74	—	—	1.58 (74)	2.34 (50)	67.6 (74)
Massachusetts (Portnoy and Dodge 1980)	9	3.33 (9)	2.67 (3)	2.00 (5)	2.50 (4)	80.0 (5)
Central Ontario (Armstrong and Euler 1982)	6	—	—	1.8	2.2	83.3 (6)

habitat, but were less successful than pairs of adults. Consequently, nest success for BWH is less affected by habitat at the nest than by age of nesters. Newton (1976) noted a similar situation in regard to habitat for the European Sparrowhawk and suggested that the higher success observed in the best habitat was due to considerably higher prey availability. We did not quantify prey availability in different hunting habitats.

Many researchers have shown that species diversity and individual species densities are often greater in an ecotone than in adjacent habitats. Our observations agree with Keran (1978) and Titus and Mosher (1981) that BWH hunt the forest edge, particularly near wetlands or ponds in response to higher prey density. Gates and Gysel (1978) documented an increased density of open-nesting passerines in a field-forest ecotone even though there was a concomitant decrease in fledging success, apparently because of predation. In fact, as for passerines, BWH nesting success declined near forest edge, possibly because of the increased likelihood of predation.

RSH. RSH populations in western New York appear uniformly less successful than those in other regions (Table 12), and the species should be considered as threatened in New York. Weather and human disturbance can be major causes of reproductive failure for RSH (Craighead and Craighead 1956; Henny et al. 1973; Wiley 1975; Sharp and Campbell 1982), and Raccoons and GHO are known predator threats (Craighead and Craighead 1956; Wiley 1975; Bednarz 1979; Portnoy and Dodge 1979). However, only Wiley (1975) recorded GHO predation more than once. In contrast the GHO appears to be the major reason for the low success of RSH in western New York.

Breeding Strategies of the Broad-winged Hawk. Newton (1977) discussed trends in breeding strategy over evolutionary time in small, short-lived raptors having large clutches, high breeding rates, and early maturity ("r-selection," MacArthur and Wilson 1967 and many later references) and in large, long-lived raptors having small clutches, low breeding rates and late maturity ("k-selection"). Although these terms, and the theory associated with them, have undergone considerable discussion and controversy, they still can be validly used to represent two contrasting patterns of reproduction at opposite ends of a continuum. Compared to buteos, BWH in western New York tends toward an "r"-strategy as evidenced by high adult mortality, early maturity, and seeming early recruitment into the breeding population. Relatively high reproductive failure for BWH in some (lesser-quality) habitats and in years of apparent low food supplies may or may not reinforce an r strategy for BWH reproduction, but would not select against it.

O'Connor (1977) theorized that birds might evolve 1 of 3 breeding strategies by which to maximize reproductive effort within a given year: clutch adjustment, brood reduction, or resource storage. Going further, Hirschfield and Tinkel (1975) suggested that an organism might be flexible, and to maximize contributions to future generations, adjust reproductive strategy from one breeding season to the next, based on environmental constraints. Indeed, Howe (1976) showed that the Common Grackle can simultaneously utilize 2 strategies. Clearly, the BWH often shows brood reduction as do many other raptors (see Newton 1977 for a general review). High adult BWH mortality (Crocoll and Parker, pers. obs.) probably puts an adaptive premium on maximum, annual reproductive output, unlike some other raptors (Newton 1979; Newton et al. 1981; Forsman et al. 1984).

For the BWH it might also be advantageous to have a way to optimize reproductive effort in any year to adjust for unpredictable food variability; to move away from being an extreme r-strategist and use clutch adjustment. O'Connor (1977) predicted clutch adjustment would occur when eventual food supply for young was predictable prior to egg laying and likely to remain stable throughout the nestling period. Lack (1966) noted for the Common Swift (*Apus apus*) that optimal clutch size in one year might not be the optimal clutch size in another year. For our study average BWH clutch size was significantly higher in 1979 ($\sim$3) than 1978 ($\sim$2). Diet analysis indicated that food was not as plentiful in 1978 as 1979, and brood reduction only occurred in clutches of 3 and 4, never for 2. We suggest that a lower food supply in 1978 may have, in part, determined the lower reproductive effort by triggering use of a clutch adjustment strategy. Brood reduction would be the more significant and functioning strategy in years of initially higher food supplies. Although our study is insufficient to confirm this generalization, the BWH appears to be comparatively an r-selectionist, capable of optimizing its reproductive effort in any given year by employing the brood reduction strategy, but with occasional lessening of an r-selection pattern by resort to clutch adjustment. Additional long-term studies of reproduction and prey availability could determine if BWH or other raptors regularly resort to such complex strategies, and the terms r- and k-selection may prove inadequate to describe some breeding patterns.

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LITERATURE CITED

ANONYMOUS. 1984. Status reports: state endangered and threatened raptor species. *The Eyas* 7(3):17–20.

APANIUS, VICTOR. 1977. Red-shouldered Hawks in juvenile plumage nest successfully. *Auk* 94:585.

ARMSTRONG, EDWARD AND DAVID EULER. 1982. Habitat usage of two woodland Buteo species in central Ontario. *Can. Field-Nat.* 97:200–207.

BEDNARZ, JAMES C. 1979. I. Productivity, nest sites and habitat of Red-shouldered and Red-tailed Hawks in Iowa and II. Status, habitat utilization and management of Red-shouldered Hawks in Iowa. M.S. Thesis, Iowa State University, Ames, IA.

——— AND JAMES J. DINSMORE. 1981. Status, habitat use and management of Red-shouldered Hawks in Iowa. *J. Wildl. Manage.* 45:236–241.

——— AND ———. 1982. Nest sites and habitat of Red-shouldered and Red-tailed Hawks in Iowa. *Wilson Bull.* 94:31–45.

BENT, A. C. 1937. Life histories of North American birds of prey. Volume 1. Reprint, Dover Publications, New York, NY.

BROWN, CHARLES R. 1978. Clutch size and reproductive success of adult and subadult purple martins. *Southwest. Nat.* 23:597–604.

BROWN, LESLIE H. 1966. Observations on some Kenya eagles. *Ibis* 108:531–572.

——— AND DEAN AMADON. 1968. Eagles, hawks and falcons of the world. McGraw-Hill, New York.

BROWN, W. H. 1971. Winter population trends in the Red-shouldered Hawk. *Amer. Birds* 25:813–817.

BURNS, FRANK L. 1911. A monograph of the Broad-winged Hawk (*Buteo platypterus*). *Wilson Bull.* 23: 139–320.

CRAIGHEAD, JOHN J. AND FRANK C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. The Stackpole Co., Harrisburg, PA and Wildl. Manage. Institute, Washington, DC.

CRAWFORD, RICHARD D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed Blackbirds. *Wilson Bull.* 89:73–80.

CROCOLL, SCOTT T. AND JAMES W. PARKER. 1986. Canadaway Raptors. *The Conservationist* 41:36–41.

——— AND ———. 1988. The life and times of the Red-shouldered Hawk. *The Conservationist* 43:41–45.

FISHER, HARVEY I. 1975. The relationship between deferred breeding and mortality in the Laysan Albatross. *Auk* 92:433–441.

FORSMAN, E. D., E. C. MESLOW AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl. *Wildl. Monogr.* 87. 64 pp.

FULLER, MARK R. 1979. Spatiotemporal ecology of four sympatric raptor species. Ph.D. Dissertation, University of Minnesota, Minneapolis, Minnesota.

GATES, J. EDWARD AND LESLIE W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.

HENNY, C. J., F. C. SCHMID, E. L. MARTIN AND L. L. HOOD. 1973. Territorial behavior, pesticides, and the population ecology of Red-shouldered Hawks in central Maryland, 1943–1971. *Ecology* 54:545–554.

HIRSHFIELD, MICHAEL F. AND DONALD W. TINKLE. 1975. Natural selection and the evolution of reproductive effort. *Proc. Nat. Acad. Sci. U.S.A.* 72:2227–2231.

HOWE, HENRY F. 1976. Egg size, hatching asynchrony, sex and brood reduction in the Common Grackle. *Ecology* 57:1195–1207.

HOWELL, J., B. SMITH, J. B. HOLT, JR. AND D. R. OSBORNE. 1978. Habitat structure and productivity in Red-tailed Hawks. *Bird-Banding* 49:162–171.

JANIK, CYNTHIA A. AND JAMES A. MOSHER. 1982. Breeding biology of raptors in the central Appalachians. *Raptor Res.* 16:18–24.

KERAN, DOUG C. 1976. Nest site selection by the Broad-winged Hawk in north central Minnesota and Wisconsin, 1971–1974. M.S. Thesis, St. Cloud State University, St. Cloud, MN.

———. 1978. Nest site selection by the Broad-winged Hawk in north central Minnesota and Wisconsin. *Raptor Res.* 12:15–20.

KIMMEL, VICKI L. AND LEIGH H. FREDRICKSON. 1981. Nesting ecology of the Red-shouldered Hawk in southeastern Missouri. *Trans. Missouri Acad. Sci.* 15:21–27.

LACK, DAVID. 1966. Population studies of birds. Clarendon Press, Oxford.

———. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LUTTICH, S. N., L. B. KEITH AND J. D. STEPHENSON. 1971. Population dynamics of the Red-tailed Hawk (*Buteo jamaicensis*) at Rochester, Alberta. *Auk* 88:73–87.

LYONS, DAVID M. AND JAMES A. MOSHER. 1987. Morphological growth, behavioral development, and parental care of Broad-winged Hawks. *J. Field Ornithol* 58:334–344.

MACARTHUR, ROBERT H. AND EDWARD O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

MASON, TIMOTHY. 1980. The Red-shouldered Hawk of the Yellow River. *Iowa Bird Life* 50:68–70.

MATRAY, PAUL F. 1974. Broad-winged Hawk nesting and ecology. *Auk* 91:307–324.

MCINVAILLE, WILLIAM B. AND LLOYD B. KEITH. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. *Can. Field-Nat.* 88:1–20.

MORRIS, MICHAEL M. J., B. L. PENAK, R. E. LEMON AND D. M. BIRD. 1982. Characteristics of Red-shouldered Hawk (*Buteo lineatus*) nest sites in southwestern Quebec. *Can. Field-Nat.* 96:139–142.

NEWTON, IAN. 1976. Breeding of Sparrowhawks, (*Accipiter nisus*) in different environments. *J. Anim. Ecol* 45:831–849.

———. 1977. Breeding strategies in birds of prey. *Living Bird* 16:51–82.

———. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD.

———. 1986. The Sparrowhawk. T. and A. D. Poyser, Calton, England.

O'CONNOR, RAYMOND J. 1977. Growth strategies in nestling passerines. *Living Bird* 16:209–238.

PARKER, JAMES W. 1972. A mirror and pole device for examining high nests. *Bird-Banding* 43:216–218.

———. 1974. The breeding biology of the Mississippi Kite in the Great Plains. Unpublished Ph.D. Dissertation, Univ. Kansas, Lawrence.

PORTNOY, JOHN W. AND WENDELL E. DODGE. 1979 Red-shouldered Hawk nesting ecology and behavior *Wilson Bull.* 91:104–117.

PRESTON, C. R., C. S. HARGER AND H. E. HARGER. 1989 Habitat use and nest-site selection by Red-shouldered Hawks in Arkansas. *Southwest. Nat.* 34:72–78.

ROSENFIELD, ROBERT N. 1984. Nesting biology of Broad-winged Hawks in Wisconsin. *Raptor Res.* 18:6–9.

RUSCH, DONALD H. AND PHILLIP D. DOERR. 1972 Broad-winged Hawk nesting and food habits. *Auk* 89. 139–145.

SHARP, MIREK J. AND CRAIG A. CAMPBELL. 1982 Breeding ecology and status of Red-shouldered Hawks (*Buteo l. lineatus*) in Waterloo Region. *Ont. Field Biol* 36:1–10.

SHELFORD, VICTOR. 1963. The ecology of North America. University of Illinois Press, Urbana, IL.

SOKAL, ROBERT R. AND F. JAMES ROHLF. 1969. Biometry. W. H. Freeman and Company, San Francisco.

STEWART, ROBERT E. 1949. Ecology of a nesting Red-shouldered Hawk population. *Wilson Bull.* 61:26–35.

TITUS, KIMBERLY AND JAMES A. MOSHER. 1981. Nest-site habitat selected by woodland hawks in the central Appalachians. *Auk* 98:270–281.

——— AND ———. 1987. Selection of nest tree species by Red-shouldered and Broad-winged Hawks in two temperate forest regions. *J. Field Ornithol.* 58:274–283.

U.S.D.I., BUR. LAND MANAGE. 1979. Snake River Birds of Prey Special Research Report to the Secretary of the Interior. Boise District, ID.

WEEKS, HARMON P., JR. 1978. Clutch size variation in the Eastern Phoebe in southern Indiana. *Auk* 95:656–666.

WILEY, JAMES W. 1975. The nesting and reproductive success of Red-tailed Hawks and Red-shouldered Hawks in Orange County, California, 1973. *Condor* 77:133–139.

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